Hrusa, G.F. 2014. Two new subspecies of *Gilia ochroleuca* (*Gilia* sect. *arachnion*: Polemoniaceae) from southwest-central California. Phytoneuron 2014-90: 1–16.

TWO NEW SUBSPECIES OF *GILIA OCHROLEUCA* (*GILIA* SECT. *ARACHNION*: POLEMONIACEAE) FROM SOUTHWEST-CENTRAL CALIFORNIA

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ABSTRACT

One new subspecies is described, and one previously unrecognized taxon is recombined as a subspecies within *Gilia ochroleuca* M.E. Jones. **Gilia ochroleuca** subsp. **lanosa** Hrusa, **subsp. nov.**, occurs in sandy habitats within the San Rafael, Sierra Madre, and Topa Topa Mountains in the western Transverse Ranges of Santa Barbara and Ventura cos., California. It is a long-styled, rosette-forming annual, distinguished within the *Gilia ochroleuca* complex by its combination of lanate stem vestiture, monocaulic habit, and slender elongated cauline leaves with 1–2 short lobes generally at the base. **Gilia ochroleuca** subsp. **minima** (Eastw.) Hrusa, **comb. et stat. nov.**, based on *Gilia pedunculata* var. *minima* Eastw., occurs in the South Coast Ranges from central Monterey Co. to northernmost Santa Barbara Co. It is a small flowered, short-styled annual that has been mistaken for both *G. ochroleuca* subsp. *ochroleuca* and *G. minor*. Its similarity to *G. ochroleuca* subsp. *ochroleuca* appears due to parallel adaptation for self-fertilization. It bears only sectional relationship to *G. minor* and generic relationship to *G. pedunculata* Eastw. (= *G. achilleifolia* var. *multicaulis*). An emended description is provided, as the protologue described only how var. *minima* differed from *G. pedunculata*.

Verne and Alva Grant once stated that *Gilia* sect. *Arachnion*, the "cobwebby *Gilia*s", "comprises the taxonomically most complex and critical group in the genus [*Gilia*] and perhaps in the entire family Polemoniaceae" (A.&V. Grant 1956). It is thus perhaps not surprising that in sect. *Arachnion* continuing studies in both field and herbarium have now revealed previously unrecognized entities. The Grants performed complex biosystematic work including intra- and interspecific crosses and hybrid meiotic analyses (V.&A. Grant 1960), in addition to morphological study. Their classification, modified slightly over the years, proposed five major morphological units with 18 species and 37 total taxa within sect. *Arachnion*. These five units were each given the informal rank of 'Group' (equivalent to subsection) and were identified by one of the members; thus the *Gilia ochroleuca* Group comprises the diploid taxa *Gilia ochroleuca*, its four subspecies, and *Gilia cana* with its five subspecies. The *Gilia tenuiflora* Group is the most diverse and largest. It comprises eight diploid and four allotetraploid species. Among the diverse diploid species are *Gilia leptantha* with five subspecies and *Gilia tenuiflora* with four. The *Gilia tenuiflora* Group also includes the tetraploid *Gilia opthalmoides* with its three subspecies; it is the only tetraploid species with significant intraspecific structure. Finally, the *Gilia latiflora* Group comprises two diploid species, *Gilia latiflora* with six subspecies and the monotypic *Gilia diegensis*.

Experimental crosses made within the species Groups indicated that the taxa treated as subspecies were variably interfertile (V.&A. Grant 1960) with several layers of isolating mechanisms; some did not form capsules, others did not set filled seed, others only filled few seeds, in others the filled seeds did not germinate, and in still others filled seeds produced vigorous and sometimes fertile hybrids. Meiotic irregularities in the less fertile hybrid offspring were frequent and occurred in

crosses both between Groups and within Group; in *Gilia ochroleuca* subsp. *exilis* there was structural divergence between at least two populations of that subspecies. Overall, the form of the irregularities indicated both translocations and inversions were contributing to the intersterility (V.&A. Grant 1960).

Morphologically the variation among and within these Groups is also complex. Specific assignment without complete material and a relatively well-stocked and curated herbarium can be frustrating; at worst it becomes a guess. The sources of the variability, according to the hypotheses formulated by the Grant's work (A.&V. Grant 1956), largely was interspecific and inter-subspecific hybridization, occurring both within and between Groups and combined with a degree of phenotypic plasticity.

Gilia ochroleuca subsp. lanosa

On a collecting trip into western Santa Barbara Co. in 1906, Alice Eastwood collected a *Gilia* somewhere between Zaca Lake and the Sisquoc River canyon. This specimen did not receive a preliminary identification nor was it identified over the next 109 years. More collections of that *Gilia* did not arrive at the California Academy of Sciences until 1957, well after Miss Eastwood's time at the Academy had ended. Although plants referable to subsp. *lanosa* were also found in 1929 by Ralph Hoffmann near Madulce Peak in eastern Santa Barbara Co., that specimen remained unidentified at the Santa Barbara Natural History Museum herbarium (SBM, now at SBBG). Two collections from the Sespe Gorge of Ventura Co. in 1934 and 1935, deposited at POM, were likewise not identified, and were the last collections until the 1957 specimen appeared at CAS. Intensive collecting in the region by Clare Hardham, Clifton Smith, Jim Blakely and their colleagues in the late 1950s and 1960s in the same general region increased significantly the number of collections and the known range (Fig. 1). Most were identified as *Gilia ochroleuca* subsp. *bizonata* or were left unnamed. This *Gilia* first came to the author's attention in 2005 when he collected it during field work documenting the flora of the Sierra Madre Mountains of Santa Barbara Co.

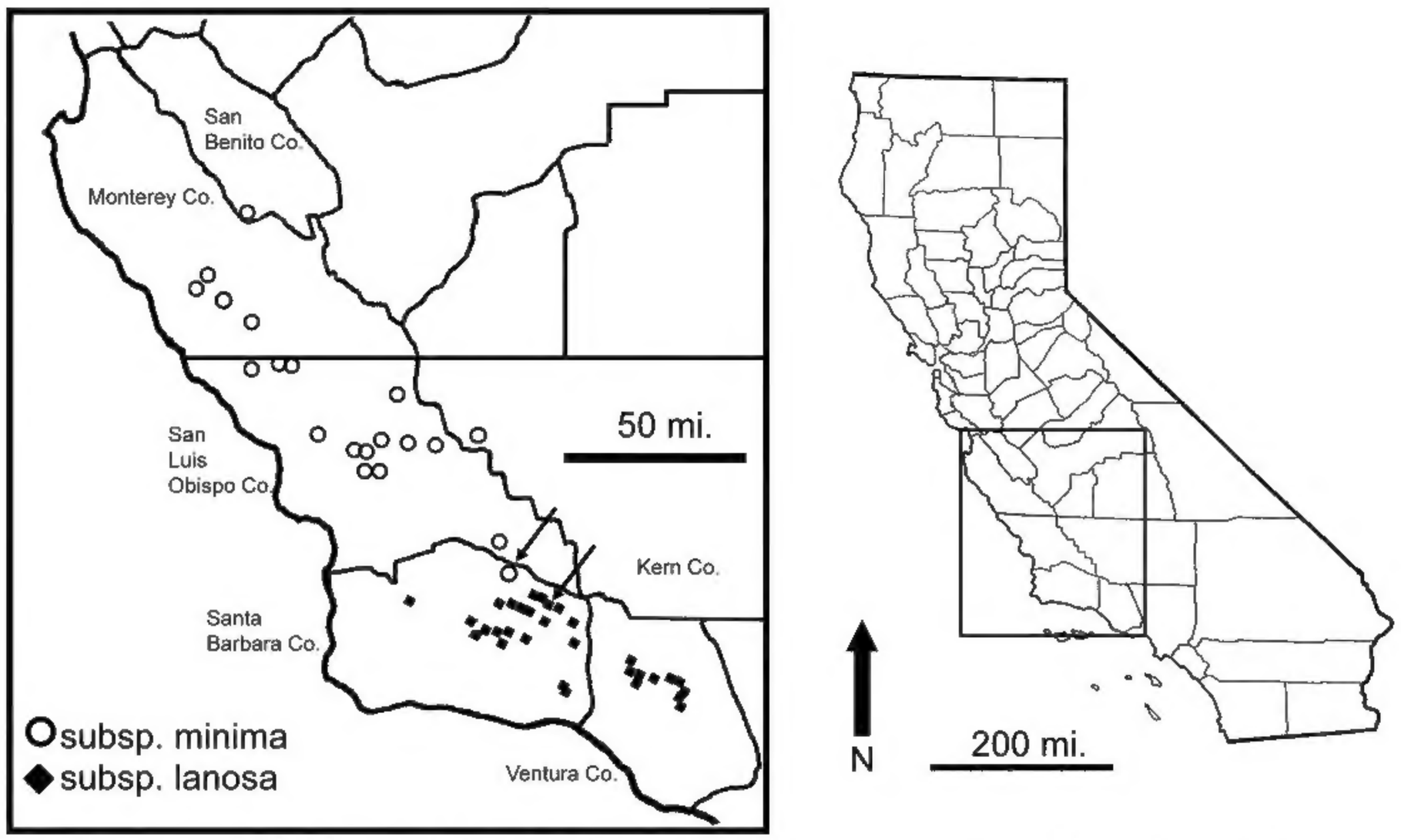

Figure 1. Known distribution of *Gilia ochroleuca* subsp. *minima* and subsp. *lanosa* in southwest-central California. Arrows indicate the type localities.

GILIA OCHROLEUCA M.E. Jones **subsp. LANOSA** Hrusa, **subsp. nov.** (Figs. 1, 2, 3A, 4, 5A-C).
TYPE: USA. California. Santa Barbara Co.: Los Padres National Forest, Sierra Madre Mountains, white colored sandstone outcrop at head of Sweetwater Canyon, immediately S of Salisbury Potrero and E of Pine Corral Potrero, at base of slope on S side of Sierra Madre Rd., 34°48'48.87" N, 119°42'01.17" W, 4773 ft (1459 m), 20 May 2010, *G.F. Hrusa 18217 & M. Beyers* (holotype: CDA; isotypes: RSA, UC, DAV, CAS, OBI, SBBG).

Annuals, plants erect, 5–50 cm tall, gen. narrow, single stemmed (unless damaged), or with poorly to moderately developed secondary branches arising from above, or sometimes near, the rosette, but most frequently without significant secondary branching below the inflorescence. **Herbage** gray to grayish green. **Leaves** of the rosette fresh or dried at flowering, numerous or few, densely or thinly cobwebby pubescent on both surfaces, petiole narrower than the blade rachis, the blade pinnately lobed or weakly bipinnate with the pinnae short-lobed near the base or shallowly bifurcate at summit, the rachis narrower to rarely broader than the length of the lobes, 1–2 mm wide when fresh, the divisions narrower than the rachis or most often about the same width, sharp-tipped. Lowermost cauline leaves pinnate, the pinnae gen. in the upper 2/3 of the leaf. Middle cauline leaves sessile, linear, ascending to appressed, densely cobwebby, 8 to 25 mm in length, terminal lobe elongated, lateral lobes reduced, short triangular and near the lf. base, <1/6 as long as the leaf blade, in exceptionally vigorous plants sometimes with a second lobe near the base or near the tip, rarely longer than the width of the leaf rachis, or the leaves simple. Upper cauline leaves shorter than middle and lower cauline, generally like the middle cauline but more frequently simple. **Flowering stems** densely cobwebby, non-glandular pubescent below the first inflorescence branches, becoming less so at maturity. **Inflorescence** divaricately branched, at maturity frequently broader than tall, the branches not cobwebby, densely glandular to thinly glandular or rarely glabrous, and with a short, densely glandular section 1–3 mm long immediately below the calyx. **Bracts** glandular, cobwebby, or both, these 2–5 mm, simple or with a <1 mm pair of lobes near the base. **Bractlets** gen. simple 2 mm to <1 mm long, rarely with a pair of small basal lobes. **Flowers** 1–2 above a bractlet; the pedicels unequal, variable in length, 3 to 20 mm long, the longest 1.5 to 6 times longer than the shortest. Uppermost longer pedicel frequently with a 1.0–1.5 mm, simple bractlet in the lower half. **Calyx** 2 to 4 mm, glabrous or if thinly cobwebby when young, becoming glabrous at maturity, frequently purple or purple-streaked, blotched or spotted. **Corolla** 7 to 12 mm long, tube equal to or slightly longer than throat, gen. exerted from calyx <1mm, white, yellow, streaked purplish or purple in the upper part, thinly glandular in the upper part or glabrous, throat gradually expanded above the tube, yellow or pale in the lower half with blue-purple markings above, the lobes pink to purple-blue, 1.8–2.3 mm Stigma at maturity barely beyond, or up to 1.5 mm beyond the anthers, its branches 0.8–1.2 mm Stamens shorter than the corolla lobes, inserted immediately below the sinus, filaments ca. equal, 0.3–1.0 mm in length. Anthers 0.3–0.5 mm, equal, pollen blue. **Capsule** ovoid, at maturity 3 to 5 mm in length, as long as, or longer than the calyx lobes by up to ¼ its length. **Seeds** 1–4 per locule, 1.4 to 2.4 mm long and 0.7–1.2 mm wide, the color reddish to yellowish brown, with vermiculate ridges.

Additional specimens examined. **California.** Santa Barbara Co.: San Rafael Mountains, trail to Manzana Creek from Zaca Lake forest reserve, 22 Jun 1906, *Eastwood 667* (CAS); sandy flat, Madulce Ranger Station, 8 Jul 1929, *Hoffmann* (SBBG); 8 mi N of Manzana [Nira] Camp Ground, 29 May 1959, *Hardham 4688* (RSA); Manzana River at Fish Creek on trail to Hurricane Deck, 20 May 1957, *Hardham 2024* (CAS, RSA, SBBG); Pine Corral Potrero, roadbank in loamy soil, 23 May 1957, *Smith 5453* (RSA, SBBG); Hurricane Deck, 23 May 1960, *Hardham 5890* (CAS, SBBG, RSA); Santa Ynez River valley, Mono debris dam at confluence of Indian and Mono Creeks, 6 May 1962, *Breedlove 2679* (CAS, UCR, RSA); Sierra Madre Mountains, Montgomery Potrero, 11 May 1962, *Chandler 724* (RSA, SBBG); Fish Creek on Manzana [River], 23 May 1962, *Hardham 10224* (CAS, RSA, SBBG); Santa Ynez Mountains, bank of fire road near mouth of Indian Creek, upper Santa

Ynez River, 23 May 1962, *Smith 6871* (SBBG); Santa Ynez Mountains, bank of fire road near mouth of Indian Creek, upper Santa Ynez River, 23 May 1962, *Smith 6868* (SBBG); E end, Hurricane Deck, 24 May 1962, *Hardham 10225* (RSA); Sierra Madre Mountains, sandy flood plain, Sisquoc River at Tepusquet Rd. crossing, 24 May 1967, *Chandler 3400-A* (SBBG); sandy, rocky area along road, E of Pine Corral Potrero, 14 May 1973, *Smith 10565* (RSA, SBBG); Pine Corral Potrero, sandy bench, incised creek canyon below Cherry Orchard and James Springs at SE edge of potrero, 34°49'12" N, 119°43'16" W, 4480 ft, 4 Jun 2005, *Hrusa & Ragan 16594* (CDA, CAS); alluvium, open spots above Manzana Creek, ca. 3 mi downstream of Nira camp, W ca. ¼ mile of Coldwater Camp, 34°47'41" N, 119°58'46" W, 1800 ft, 10 Jun 2006, *Hrusa & Dougherty 16850* (CDA); Sierra Madre Mountains, white-colored sandstone outcrop at head of Sweetwater Canyon, immediately S of Salisbury Potrero and E of Pine Corral Potrero, 34°48'48.87" N, 119°42'01.17" W, 4773 ft, 30 Apr 2008, *Hrusa 17329* (CDA, RSA, DAV, CAS); Santa Barbara Canyon at Big Pine Rd., 6 May 2008, *Gross 3345* (RSA); Manzana Creek, ca. 0.7 km E of Lost Valley, ca. 1.3 km WNW mouth Fish Creek, San Rafael Wilderness, 600 m, 34.7655° N, 119.9149° W, 7 May 2008, *Wilken & Muller 16768* (SBBG); sandy upper alluvium, Sisquoc River ca. 3/4 mi. downstream from Sycamore Camp, 34°48'39" N, 119°49'07" W, 2100 ft, 29 Apr. 2008, *Hrusa 17212a* (CAS); Sisquoc River Canyon, open gravelly slope on disintegrating conglomerate, steep N slope of pinnacle on S side of river, W of Mine Canyon confluence, ca. ¼ mile E of Cliff Camp, 34°48'57" N, 119°50'46" W, 1970 ft, 9 May 2009, *Hrusa 17817* (CDA, CAS, UC); sandy floodwash zone among shrubs, Sisquoc River Canyon between Big Bend Canyon and Mine Canyon, 34°48'57" N, 119°50'01" W, 1870 ft, 9 Jun 2011, *Hrusa & Beyers 18384* (UC); uncommon on slope below Sierra Madre Rd. between Salisbury Potrero gate and Pine Corral Potrero, 34°48'59" N, 119°42'33" W, 4870 ft, 30 Apr. 2008, *Hrusa 17313* (CDA); Sisquoc River Canyon, ca. 2 mi E of Cliff Camp, 34°48'54" N, 119°49'59" W, 1855 ft, 9 May 2009, *Hrusa 17787* (CDA, CAS, UC, RSA); Sisquoc River, sandy and rocky fresh riverwash, first river crossing upstream from Sycamore Camp, 34°48'19" N, 119°48'26" W, 2010 ft, 10 May 2009, *Hrusa 17836* (CDA, UC, RSA, CAS, SBBG); sandy hillside, behind S wall of sandstone 'amphitheatre', Sweetwater Trail, ca. 4 mi. S of Sierra Madre Rd. on ridge between Sweetwater Canyon and Forester's Leap Canyon, 34°47'50" N, 119°44'43" W, 4505 ft, 13 Jun 2009, *Hrusa 17923* (DAV, SBBG); Ventura Co.: Topa Topa Mountains, sandy soil near Wheeler's Hot Springs, 1500 ft, 1 May 1934, *Munz 13206* (RSA); Brushy Flat, Sespe Creek, 900 m, 2 May 1935, *Clokey & Anderson 6821* (RSA, SBBG); Howard Creek, Sespe, 8 May 1961, *Hardham 6955* (RSA); shale hills opposite the Sandstone Camp, Rte. 399 [Hwy 33], 4500 ft, 8 May 1961, *Hardham 6962* (CAS, RSA, SBBG); shale hills opposite the Sandstone Camp, Rte. 399 [Hwy 33], 4500 ft, 8 May 1961, *Hardham 6963* (RSA); sandy soil, upper Sespe, Rte 399 [Hwy 33], 4500 ft, 16 Jun 1962, *Hardham 10339* (CAS, RSA [as 10399], SBBG); mouth of Derrydale Creek and Sespe River, 5 Jun 1963, *Blakley 5993* (RSA, SBBG); flat on Sespe Creek Rd. between Lion and Bear Canyons, 3000 ft, 1 Jun 1966, *Pollard* (CAS); Rte. 33 near Sandstone Camp, upper Sespe watershed, 4500 ft, 2 Jun 1967, *Chandler 3485-C* (SBBG); Hwy 33 at Sandstone Campground, upper Sespe Creek watershed, 2 Jun 1967, *Smith 9676* (SBBG); sandy flat near jtn. of Cherry Creek and Sespe Creek, upper Sespe watershed, 4000 ft, 21 Jun 1967, *Chandler 3583* (SBBG); upper Cherry Creek Canyon off Hwy 399 [Hwy 33], upper Sespe Creek watershed, 21 Jun 1967, *Smith 9835* (CAS, SBBG); Chorro Grande Cyn., draining into Sespe Creek from N off Pine Mountain, near US gypsum quarry, 7 Jun 1971, *Clarke PLM-2* (RSA).

The Gilia ochroleuca Group

Gilia ochroleuca subsp. *ochroleuca*, subsp. *exilis* (Gray) Grant & Grant, subsp. *bizonata* Grant & Grant, and subsp. *vivida* (Grant & Grant) Grant & Grant (Porter 2012) are regionally widespread taxa. *Gilia ochroleuca* subsp. *ochroleuca* occupies the California Mojave Desert margins; *G. ochroleuca* subsp. *bizonata* is frequent in the Transverse ranges from its northwestern limit near Mt. Pinos in Kern and Ventura Cos. to the San Gabriel Mtns. of Los Angeles Co.; *G. ochroleuca* subsp. *exilis* is centered south of Los Angeles Co., where it is most frequent in western Riverside and San Diego Cos.; and subspecies *vivida* has perhaps the smallest range among these four taxa, being

Figure 2. A. Conditions at type locality of *Gilia ochroleuca* subsp. *lanosa.* The plants occur on the light-colored sandstone in wet years, on the margins of it in less well-watered years. The burned trees are 10–15 ft. tall *Pinus monophylla.* The type locality and much of the range of the subspecies in the Sierra Madre was burned in the 2009 La Brea fire, without obvious affects on the populations. B. Plant material and edaphic conditions on the poorly consolidated white sandstone at the type locality. Note the single flowering stem with branching only above the base, the broad basal leaf rachises, and prominent elongated cauline leaves.

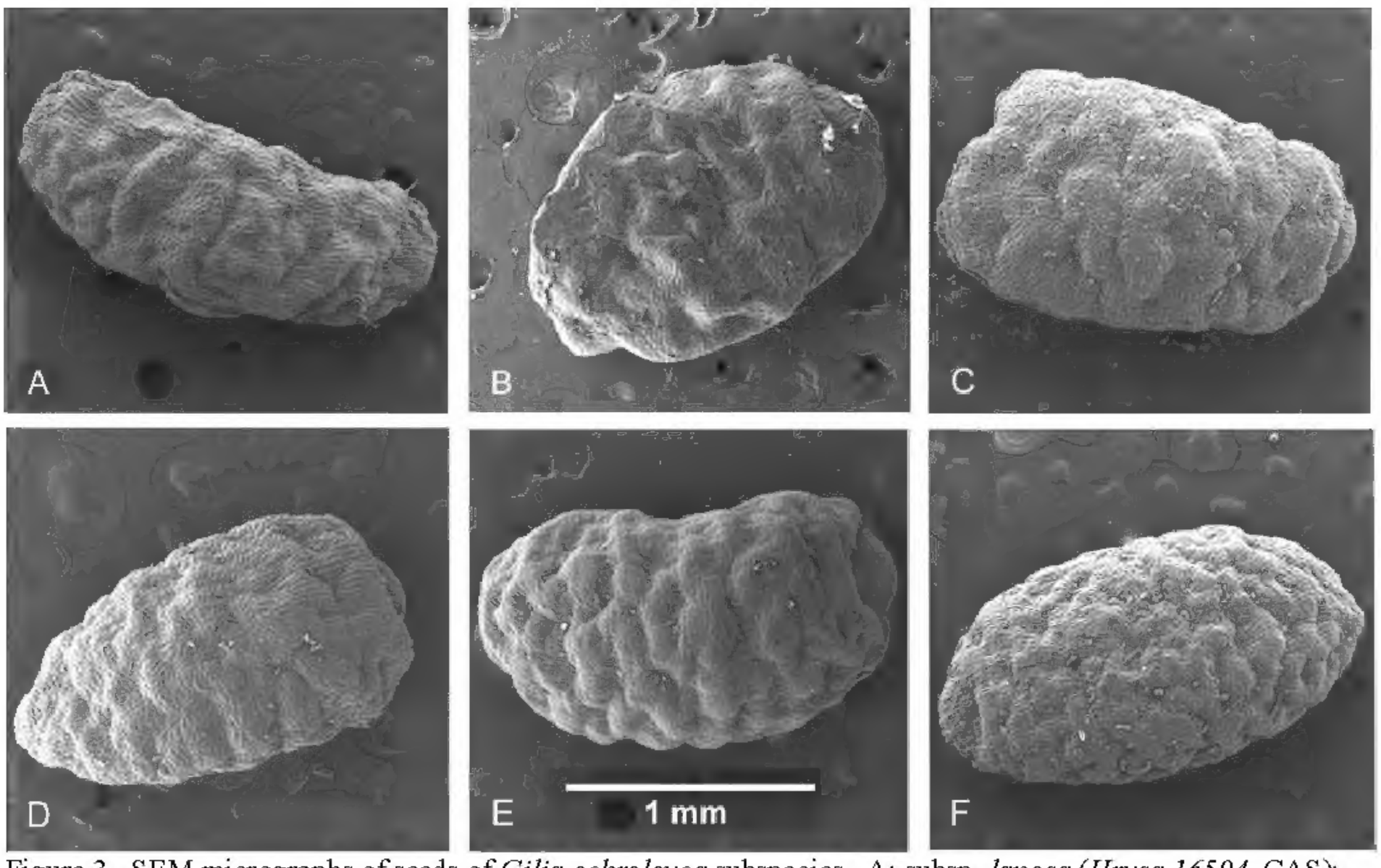

Figure 3. SEM micrographs of seeds of *Gilia ochroleuca* subspecies. A: subsp. *lanosa* (*Hrusa 16594*, CAS); B: subsp. *minima* (*Hoover 7084,* CAS); C: subsp. *ochroleuca* (*E.C. Twisselmann 8441*, CAS); D: subsp. *bizonata* (*C.B. Wolf 2438*, CAS); E: subsp. *exilis* (*M.E. Jones 6-20-1926*, CAS); F: subsp. *vivida* (*J.T. Howell 23405,* CAS). All images are scaled identically.

CA Dept. Food & Agriculture
CDA-0039613
2 cm
California Department of Food and Agriculture, Sacramento
BOTANY LABORATORY HERBARIUM
HOLOTYPUS
CALIFORNIA
SIERRA MADRE MOUNTAINS
Gilia ochroleuca ssp. lanosa Hrusa
SANTA BARBARA COUNTY: S side Sierra Madre Rd. at bottom of hill, 1/4 mi. SE of Salisbury Potrero access gate.
Loose, decomposing, pure white sandstone outcrop. Annual, flrs dark on outside, lighter inside. Flr stem monopodial, branched only above, unless damaged. Large colony.
ELEV: 4780 ft.
34°48'49"N; 119°42'2"W
May 20, 2010
G.F. Hrusa 18217
M. Beyers
Specimen Courtesy of the
Lone Mtn. Institute, O'Brien, Oreg.

Figure 4. Type specimen of *Gilia ochroleuca* subsp. *lanosa* (*Hrusa 18217*, CDA). The single flowering stem with branching only above the base and the cauline leaves with elongated terminal and reduced lateral lobes are visible diagnostic features.

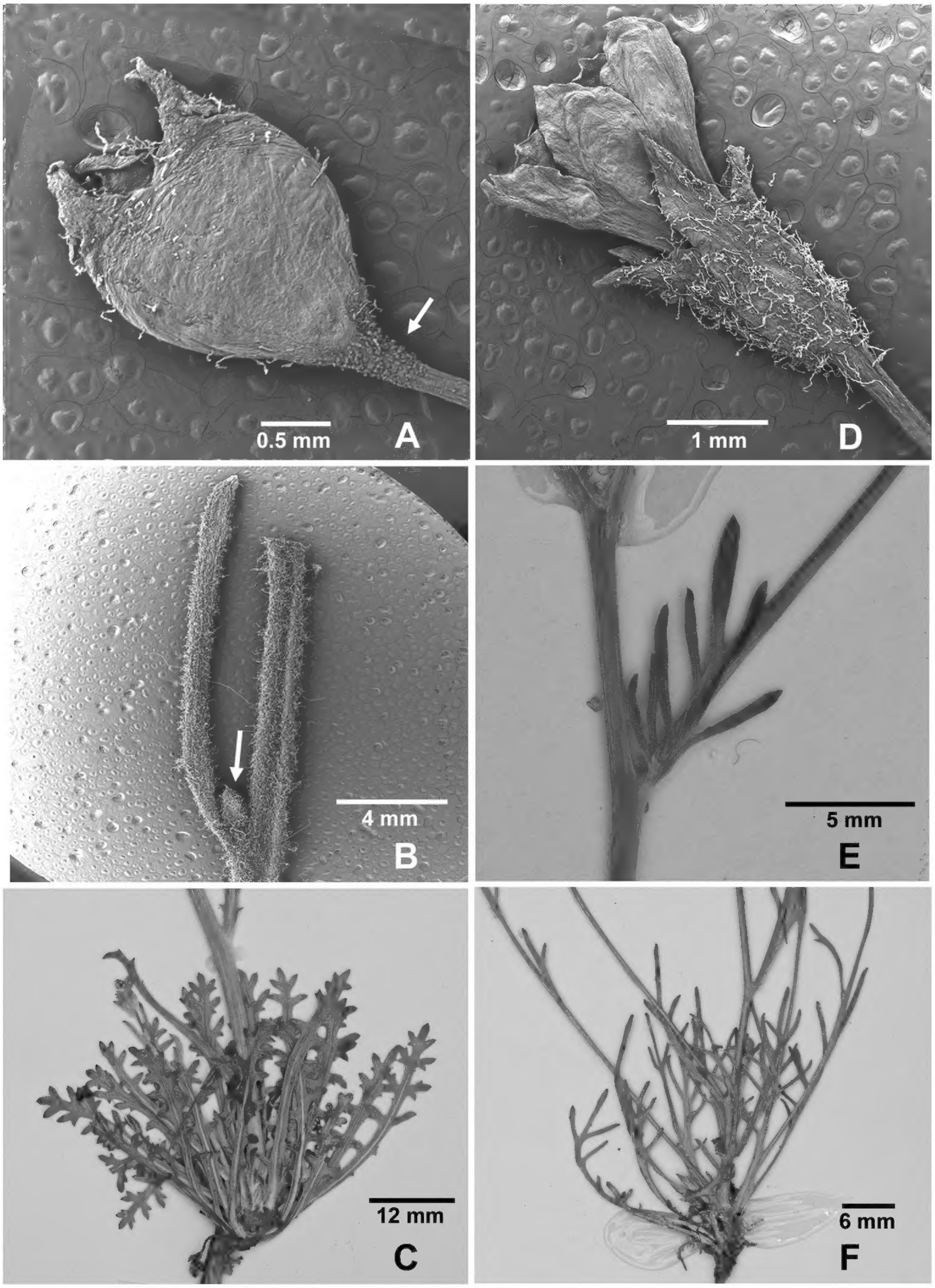

Figure 5. A-C: Distinguishing features of *Gilia ochroleuca* subsp. *lanosa*. A: Arrow indicates form and position of glandular ring at pedicel summit. B: Densely lanose cauline leaf and stem with elongated terminal lobe (also Figs. 2B, 4). Arrow indicates short lateral lobe. C: Basal leaf rosette with pinnate to weakly bipinnate leaves with broad rachis. D-F: Features of *Gilia ochroleuca* subsp. *minima*. D: Cobwebby calyx, with fully formed corolla. E: Comparative cauline leaf, typical of all subsp. of *G. ochroleuca* except subspp. *lanosa* and *vivida*. F: Basal leaf rosette, with slender, pinnate lobing.

restricted mostly to the San Gabriel Mtns. of eastern Los Angeles Co. It is perhaps important that the original formulation of the *Gilia ochroleuca* Group did not include subsp. *vivida* (Grant & Grant 1956). That taxon was originally proposed as a subspecies of *G. leptantha* in the *Gilia tenuiflora* Group and was later (V.&A. Grant 1960) transferred to the *G. ochroleuca* Group to indicate its relative interfertility with the tested members of the latter. It was anomalous in the *Gilia tenuiflora* Group, and while somewhat less so in the *Gilia ochroleuca* Group, within *G. ochroleuca* itself it is still the most distinctive among its subspecies. The taxon here proposed as *G. ochroleuca* subsp. *lanosa* is about as distinctive and may be the result of some of the same evolutionary processes elucidated experimentally for subsp. *vivida*, but which for subsp. *lanosa* can at this point only be inferred.

Within sect. *Arachnion*, the *Gilia ochroleuca* complex is distinguished by the combination of stamens inserted evenly on the corolla throat below the sinuses; a non-glandular calyx; a corolla tube as long as the throat or shorter, and barely exerted, the tube pale blue, blue purple, yellow or white, dilated sharply into the throat; the throat white or yellow at base, blue or purple distally, with a capsule at maturity that does not or barely exceeds the calyx. Even though considerable variation exists among the *G. ochroleuca* subspecies, subsp. *lanosa* is readily distinguished from the five named taxa in the complex (including subsp. *minima* described below) by the following: (1) terminal lobe of cauline leaves elongated, with 1–2 pairs of short, triangular leaf lobes generally at the leaf base, these in length not or barely exceeding the rachis width (Fig. 5B), vs. cauline leaves with several pinnate divisions, gen. at least 3–5x longer than the rachis width (Fig. 5E); (2) a persistent dense lanate tomentum on the stems and cauline leaves below the inflorescence (Figs. 4, 5B), vs. a less dense tomentum that disappears as the plant matures persisting only on the cauline leaves, or the stems glabrous; (3) glandular or mixed glandular and lanate bractlets, vs. bractlets glabrous or lanate only; (4) a single flowering stem per rosette with any branching only above the stem base (Figs. 2B, 4), vs. plants with multiple stems from the rosette (rarely otherwise); (5) a 1–3 mm dense patch of glands on the pedicel immediately below the calyx (Fig. 5A), vs. absent among the remaining taxa or in similar form of inconsistent occurrence in subsp. *exilis*; and (6) relatively elongated seeds, the length generally at least 2 times the width. Figure 3 displays mature, well-developed seeds of subsp. *lanosa* in comparison to those of the other *G. ochroleuca* subspecies.

Alva Day annotated one herbarium sheet as *Gilia ochroleuca* subsp. *bizonata* "variant with narrow corolla throat and small lobes." A small survey of lobe length against corolla length between subspp. *lanosa* and *bizonata* revealed no significant differences. The abrupt transition from tube to throat that distinguishes *G. ochroleuca* as a whole is indeed generally less markedly developed in subsp. *lanosa*, but among and within individuals there is considerable variation in the feature and it is not reliably diagnostic. Subspecies *lanosa* is readily distinguished from subsp. *bizonata* by its dense lanate tomentum, glandular inflorescence, broad basal leaf rachis and divisions, and single flowering stem. Subspecies *bizonata* is mostly glabrous, has narrow leaf divisions, and almost always has several or many stems originating at the rosette. The only seeming morphological similarity of subsp. *lanosa* to any other *ochroleuca* variant, beyond the typical stamen and corolla configuration, is with subsp. *exilis*; both taxa may have a dense 1–3 mm wide patch of glandular trichomes at the pedicel summit (Fig. 5A), a feature absent in subspp. *bizonata*, *minima*, and *ochroleuca* but which does appear in several other taxa of sect. *Arachnion*. In subsp. *exilis* the similar glandular ring is inconsistently present and when present is less dense and less sharply delimited than it is in subsp. *lanosa*. Likewise if the glands on the inflorescence rachis in subsp. *vivida* are particularly dense below the calyx they may at times also resemble the glandular ring in *lanosa* or *exilis*. In the opinion of this author these features are not directly homologous. However, their glandular rings may share a similar derivation via interspecific gene flow. Subspecies *lanosa*, *vivida*, and *exilis* otherwise share few features. Compared to subsp. *lanosa*, subsp. *exilis* is especially variable as to basal leaf divisions: these may be weakly bipinnate, pinnate, or simple, but the divisions, when present, are always slender

and generally more than 5 times longer than the rachis width, similar to those of subspecies *minima* (Fig. 5F). The basal leaves of subspecies *lanosa* are pinnate or shallowly bipinnate, with the rachis and lateral divisions broader than in subsp. *exilis* and from less than 1 to (rarely) 4–5 times as long as the primary rachis width (Figs. 2B, 4, 5C). In vigorous specimens, the broad leaf rachis of subsp. *lanosa* is somewhat similar to that of subspecies *vivida* although never tripinnate. Overall, subsp. *lanosa* can be distinguished from subsp. *vivida* by (1) its upright simple stem vs. multiple stems spreading from the base; (2) its non pungent rosette leaves that are never more than bipinnately compound, vs. pungent tipped leaf divisions with leaves up to tripinnately compound; (3) basal leaf tomentum predominantly on the adaxium, vs. the leaf tomentum concentrated on the abaxial surface in subsp. *vivida*; and (4) its elongated and overall longer cauline leaves without pungent tips, contrasts with the shorter and pungently tipped leaves of subsp. *vivida*. It is separable from subspecies *ochroleuca*, *exilis*, *minima*, and *bizonata* by its rosette leaf divisions with broad rachis. A single unusual specimen of subsp. *exilis* from Riverside Co. (*Peirson 921*, CAS, RSA) had a single terminal flowering stem and reduced cauline leaf lobes. It could be distinguished from *lanosa* by its slender, simple basal leaves and non-lanate stems.

Alva and Verne Grant (1956, 1960) suggested the hypothesis and supported it with experimental data — that the exceptionally broad and tomentose rosette leaves of subsp. *vivida* were derived via gene flow from somewhere in the *Gilia cana* and/or *Gilia leptantha* complexes (members of the *Gilia ochroleuca* and *Gilia tenuiflora* Groups, respectively). Indeed, the basal rosette of subsp. *vivida* can be matched by those of several subspecies of *G. cana*. The basal rosette of subsp. *lanosa* is less divided and less tomentose than that in subsp. *vivida*; it bears considerable resemblance to those in the *Gilia leptantha* complex (*Gilia tenuiflora* Group) and in some individuals to those in the *Gilia latiflora* Group, which are generally simply pinnate with a broad rachis. Morover, the ring of glandular hairs below the calyx is an occasional feature of taxa in both the *Gilia cana* and *Gilia latiflora* complexes. It is possible that at least some of the distinctive variation in subsp. *lanosa* is the result of gene flow from *G. cana*, *G. leptantha*, *G. latiflora*, or some other current or extinct taxon of sect. *Arachnion*. The form of the cauline leaves in subsp. *lanosa*, with their reduced lateral lobes and elongated central lobe is not known, however, in any other member of the section and suggests the possiblity that its cauline leaf form has developed independently. One is struck by the similarity of shape between these cauline leaves and the shape of the uppermost floral bracts throughout sect. *Arachnion*. A hypothesis of the elaboration of previously reduced floral bracts to become the cauline leaves of subsp. *lanosa* is, at present, purely conjectural.

Gilia ochroleuca subsp. *lanosa* is restricted to the San Rafael, Sierra Madre and Topa Topa Mtns. in Santa Barbara and Ventura cos. (Fig. 1). It is most common about the south sides of the potreros and associated sandy ridges along the south face of the summit of the eastern Sierra Madre (Fig. 5A); it is also found on the sandy floodplain of the middle reaches of the Sisquoc River that drains the south face of the Sierra Madre. Indeed it was probably along the Sisquoc River floodplain that Miss Eastwood discovered the plant. It is less common in the next parallel drainage to the south, (the Santa Ynez River) but is frequent in the Sespe River Gorge of the Topa Topa Mountains about 25 miles east in Ventura Co. Its primary habitat is on relatively sterile, sandy soils (rarely on gravel), within oak woodlands, chaparral, and openings in pinyon pine (*Pinus monophylla*) forest (Fig. 2A). The majority of the known populations occur within the San Rafael Wilderness, a roadless watershed preserve covering the headwaters of the Sisquoc River and Manzana Creek. Wilderness designation includes the south face of the Sierra Madre and north face of the San Rafael Mountains.

As frequently seen in annual plants, subsp. *lanosa* growing under stress or other dwarfing conditions responds by not only reducing the size of the plant body but by simplifying its complexity. Stressed dwarfs often have rosette leaves with few or no divisions, have few hairs of any kind, may lack the distinctive glandular ring below the calyx (Fig. 5A), and have few rosette leaves. These

specimens can be extremely difficult to identify with certainty. Clearly, plastic responses in this taxon are as frequent as expected in an annual plant growing only during the variably moist California spring season.

From a conservation standpoint, in spite its limited distribution *Gilia ochroleuca* subsp. *lanosa* is quite secure. Its range is mostly within an established National Wilderness area. Some of the populations are large and there are no threats to any of those in the part of the Sierra Madre Mts. that does not have wilderness status. Those in the Topa Topa Mts. may not be as secure but at present, aside from their existence on and near a State Highway roadside, there appear not to be any immediate threats.

Subspecies *lanosa* is named for the dense lanose indument on the stems up to the first inflorescence branches, especially dense in the early season. The density and coverage of this indument distinguishes it from all other subspp. of *Gilia ochroleuca* and suggest possible gene flow from contact with plants referable to the generally tomentose *Gilia cana* complex. The lanate indument generally thins as the plant ages, and older, fruiting specimens may show this characteristic feature only on the lowermost stem and/or only on the middle cauline leaves and in that feature appear like subsp. *exilis* or subsp. *vivida*. The indument is most visible in Fig. 5B and on the type specimen (Fig. 4).

In the protologue to *Gilia pedunculata* var. *minima*, Eastwood cited the *G. pedunculata* var. *pedunculata* description, which is that of a different taxon (now *G. achilleifolia* subsp. *multicaulis*), with comments to accomodate the perceived form of var. *minima*. For that reason an emended description of *G. pedunculata* var. *minima* is provided here.

GILIA OCHROLEUCA M.E. Jones subsp. **MINIMA** (Eastw.) Hrusa, **comb. et stat. nov.** (Figs. 3B, 6). *Gilia pedunculata* Eastw. var. *minima* Eastw., Bot. Gaz. 37: 447. 1904. *Gilia peduncularis* Eastw. ex Milliken var. *minima* (Eastw.) Brand, Pflanzenreich, Heft 27: 108. 1907. **TYPE: USA. California.** Santa Barbara Co.: Cuyama, 7 May 1896, *A. Eastwood s.n.* (holotype: CAS 00123859, high res. digital image!). An isotype specimen at B (cited by Brand 1907) may not have survived World War II. Not *Gilia minima* (Nutt.) Gray, Proc. Amer. Acad. Sci. 8: 268. 1870 (based on *Navarretia minima* Nutt.).

Annual, erect, 5–25 cm. tall, upright, slender, single or more frequently multi-stemmed. **Stems** non-glandular, cobwebby pubescent below and at the nodes, occasionally the stems thinly cobwebby, otherwise mostly glabrous. **Basal leaves** in a sparse rosette, pinnate, glabrous or the adaxium cobwebby pubescent near the base, the lobes linear, two to six or more on each side, gen. not paired, the lobes becoming slightly broader towards the obtuse tip, 5–10x or more longer than the width of the rachis. **Cauline leaves** pinnate, sessile, 8 to 15+ mm in length, the pinnae of 2–4 linear lobes from near the leaf base, these ½ or more as long as the leaf blade, 8–10 times in length the width of the rachis, glabrous or most often cobwebby in the lower parts, obtuse at the lobe tips, not pungent. **Inflorescences** divaricately branched, cobwebby at the nodes, thinly glandular to glabrous above, rarely cobwebby; when the rachis glandular it is without a ring of glands at the pedicel summit. **Bracts** with a single pair of lobes near the base, these shorter to as long as the bract, cobwebby pubescent to glabrate, the hairs gen. restricted to the base of the leaf and the associated node. Upper bracts reduced and frequently simple above, 1.5–5 mm in length. **Flowers** 1–2(–3) above a nodal bractlet, pedicels unequal. **Calyx** 2.0 to 2.5 mm, densely to thinly cobwebby, often becoming less so in age, the ribs green or purple throughout or purple only in the lower half; the membrane smooth, not folded, purple spotted, streaked, or purple throughout, both the rib and membrane pigments frequently faded in aged herbarium specimens. **Corolla** 2 to 4 mm in length. Tube included in the calyx, equal to or slightly longer than the throat. The tube pale yellowish or white, the throat pale with a small yellow zone or spots near the summit (as per label data), the limb

pale or dark blue, frequently streaked, 1 1.5 mm in length. **Style** maturing among the anthers, the stigma lobes 0.2 0.3 mm long. **Stamens** inserted immediately below the sinus, shorter than the corolla limb, filaments equal, 0.1 0.2 mm **Anthers** 0.1 0.2 mm, equal, pollen blue. **Capsule** smooth, ovoid at maturity, 2.8 to 3.2 mm in length, as long as or shorter than the calyx lobes. **Seeds** 1 3 per locule, 1.2 to 1.6 mm long and 1.0 1.2 mm wide, orange-brown, transverse ridges few uneven.

Additional collections examined: **California.** Kern Co.: Summit of Messa Ridge [W of Carneros Rocks], Temblor Mountains, *Quercus douglasii* association, 3400 ft, 12 May 1955, *Twisselmann 1965* (CAS); Monterey Co.: Jolon, 4 Apr 1915, *Eastwood* (CAS); Santa Lucia Mountains, sandy soil, N slopes, *Quercus douglasii* assoc., hills along the San Antonio, Pleyto, [Pleyto submerged in San Antonio Reservoir, 1965], 28 Mar 1960, *Hardham 5258* (CAS504101, RSA140764; not *Hardham 5258* CAS871396, RSA555426); Santa Lucia Mountains, sandy N slope opposite Bee Rock (S side of road), 1000 ft, 28 Mar 1960, *Hardham 5258* (RSA555426, CAS871396; not *Hardham 5258* CAS504101, RSA140764); Santa Lucia Mountains, sandy bed of river ca. 2 mi N of San Antonio Mission, Sulphur Creek Canyon, 7 Apr 1960, *Hardham 5401a* (CAS, RSA); hills N of San Antonio Mission, 10 Apr 1960, *Hardham 5369* (RSA); same data, *Hardham 5469* (CAS, SBBG); San Benito Co.: San Lorenzo Creek near jtn. with San Benito River, 2000 ft, 1 May 1933, *Ferris 8367* (DS, RSA); San Luis Obispo Co.: El Dorado School, Santa Margarita, 11 May 1933, *Wall s.n.* (CAS); in coarse sand, Atascadero, 29 Mar 1947, *Hoover 6783* (UC); sandy flat, Yaro Creek district, N of Pozo, 10 Apr 1947, *Hoover 6992* (CAS, UC); on sandy flats, upper Toro Creek, N of Pozo, 26 Apr 1947, *Hoover 7084* (CAS, UC); Fernandez Creek, near N base of La Panza Range, 23 Mar 1947, *Hoover 6727* (CAS, UC); on sandy flat in area swept by fire last summer, Upper Navajo Creek, La Panza Range, 12 Apr 1947, *Hoover 6909* (CAS, UC); rd. between El Dorado School and Pozo at Yaro Creek bridge ca. 7 mi N of Pozo, 25 May 1955, *Ferris 12835* (DS); hills between San Juan River and Carissa Plains, Paso Robles-Simmler Rd, 28 Apr 1958, *Hardham 3132* (CAS, RSA, SBBG); Santa Lucia Mountains, low sandy depression in full sun, Cantinas Creek, 800 ft, 4 Apr 1960, *Hardham* 5299 (CAS, RSA, SBBG); Santa Lucia Mountains, N slope, Bee Rock, 28 Mar 1960, *Hardham 5250* (SBBG); bare sandy soil, *Pinus sabiniana* woods, intersection Cammatta Road and Shell Creek Road, 8 Apr 1960, *Hardham 5365* (CAS, RSA, SBBG); sandy bed of Huero Huero R. east branch, near Calf Canyon Rd. (S of Creston), 10 May 1963, *Hardham s.n.* (CAS); Bedell Ranch, 5 mi. SE of Creston, 1150 ft, 24 Apr 1969, *Twisselmann 15153* (CAS); California Dept. Fish & Game Ecological Reserve, N side Cuyama Valley on lower S face of Caliente Range, openings in *Atriplex canescens* scrub, on broad sandy ridge, 35°03'34.26" N, 119°54'35.25" W, 1915 ft, 3 Apr 2008, *DFG anon.* (DAV).

Examination of *Gilia* specimens from San Luis Obispo and Santa Barbara Cos. revealed that a diminutive form from the interior of the South Coast Ranges was clearly within the *Gilia ochroleuca* Group but occurred north of its reported range and with a distinctive morphology. Herbarium specimens were sometimes determined (and annotated) by Alva Day [Grant] as a "small-flowered form of *Gilia bizonata*," while others were annotated by Clare Hardham as a "self-pollinating form of *Gilia exilis*." They were mentioned by both Grant and Grant (1956, p. 224) and Hoover (1970, p. 227, under *Gilia minor*), neither of whom drew further taxonomic conclusions.

A further survey of existing *Gilia* types from central California found that the type of *Gilia pedunculata* Eastw. var. *minima* Eastw. represented this entity. Eastwood described the variety as "similar to the preceding [*G. pedunculata* — *G. achilleifolia* var. *multicaulis*] in every way, but flowers and fruits less than half as large, and whole plant smaller" (Eastwood 1904). However, the type specimen of var. *minima* is not at all like *G. pedunculata*. Rather than having single-flowered inflorescences on long peduncles, it has an open, multiflowered, divaricately branched inflorescence with spreading pedicellate flowers. Among the listed exsiccatae the four individuals on the type sheet

(Fig. 6) were among the most robust specimens seen of this subspecies. All but a few individuals on the herbarium sheets cited above are more slender, less branched, and of smaller stature than the type.

Figure 6 Type specimen of *Gilia pedunculata* subsp *minima* = *G. ochroleuca* subsp *minima* (*Eastwood s.n.*, CAS)

Gilia ochroleuca is readily separated from *G. pedunculata* (= *G. achilleifolia* var. *multicaulis*) by many features, the following most notable: pedicellate vs. essentially sessile flowers; divaricate, open, multiflowered inflorescences vs. capitate inflorescences with variable numbers of flowers per capitulum — including the occasional reduction to a single flowered inflorescence as in the *G. pedunculata* type; and leaves in a basal rosette, rapidly diminishing upwards into bracts versus in var. *multicaulis* the leaves not in a basal rosette, stems leafy, the leaves little reduced upwards.

Subspecies *minima* most resembles the small-flowered subsp. *ochroleuca* of the Mojave Desert, and the type specimen was so annotated by Alva Day in 1976 (Fig. 6). Another specimen, collected near "Pozo, San Luis Obispo Co." by R.S. Ferris (CAS) was annotated by Day as an undescribed taxon, "distinct from subsp. *ochroleuca*." Like the typical subspecies, *minima* is short-styled; the style and stigma do not extend beyond the anthers, and mature flowers usually have the stigmas coated with pollen grains. Subspecies *minima* is usually more gracile than subsp. *ochroleuca*, the leaf divisions have obtuse rather than acute tips, and subsp. *minima* more frequently has simple bracts, while in subsp. *ochroleuca* the inflorescence bracts are pinnate or subpalmate up to their distal limit. The mature seeds of subsp. *minima* are foreshortened in comparison to the remainder of *G. ochroleuca*, being usually only about 1.2–1.5 times as long as wide (Fig. 5B), while those of subsp. *ochroleuca* are about 2 times as long as wide (Fig. 5C; also Johnson et al. 2004). In subsp. *minima* the calyx may be thinly cobwebby or densely and persistently so with the tomentum thinning only at full fruit maturity (Fig. 5D); in subsp. *ochroleuca* the calyx is generally glabrous from the beginning, although immature calyces may have a few cobwebby hairs. The membrane between the calyx ribs of subsp. *minima* is wholly or in part purple in color, being solid, streaked, or colored only in the lower half; only rarely is it uncolored. In subsp. *ochroleuca* it is always uncolored (white). The inflorescence branches of subsp. *minima* are completely glabrous or have glands scattered thinly throughout, while in subsp. *ochroleuca* the inflorescence branches are more or less glandular only immediately above each node. Grant and Grant (1956) considered the apparent similarity of subsp. *minima* to *G. ochroleuca* subsp. *ochroleuca* to be a case of parallel evolution and interpreted subsp. *minima* as a "reduced form of *G. o.* [subsp.] *bizonata*." The degree of its relationship with subsp. *bizonata* is at present not understood but it differs from that subspecies in its smaller corollas, included style, persistently cobwebby calyx, foreshortened seeds, fewer basal rosette leaves, and obtuse-tipped leaf divisions.

In the spring of 1947, Robert F. Hoover collected subsp. *minima* five times in the La Panza Range of San Luis Obispo Co. He discussed these plants and ultimately interpreted them as *Gilia minor* V. & A. Grant (Hoover 1970). A mixed sheet (*Hardham 3132*, RSA) collected in the San Juan Hills west of the northern part of Carrizo Plain indicates that *G. minor* is at least occasionally sympatric with subsp. *minima*. *Gilia minor* is also present in the adjacent Caliente Mtns. and on the hilly margins of Carrizo Plain itself. Compared to subsp. *minima* it is similarly small-flowered, short-styled, and self-pollinated. It is well differentiated from subsp. *minima* by its glandular, non-cobwebby calyx, unequal stamens, shorter and more numerous basal and cauline leaf divisions, and mature capsule about twice as long as the calyx. In contrast, all forms of *G. ochroleuca* have a non-glandular calyx, equal-length stamens, and a capsule slightly shorter than to barely exceeding the fruiting calyx. Hoover (1970) listed these plants as distributed only east of the Salinas Valley in the region between Atascadero and Pozo. He did not cite the plants from west of the Salinas Valley collected by Hardham. Monterey County specimens of *G. ochroleuca* were listed by both Howitt and Howell (1964) and Matthews (1997) as subsp. *bizonata*. The specimen(s) cited by Howitt and Howell from "near San Antonio Mission" are subsp. *minima*, but the single known collection cited from the "Palisades of the Nacimiento River" (*Hardham 5772*, CAS, RSA) is a different, still uncharacterized entity within the *Gilia ochroleuca* complex. Only the Palisades location (as "Hunter-Liggett") was mentioned in Matthews (1997). Genuine subsp. *bizonata* does not occur in either San Luis Obispo or Monterey Cos. *Gilia clivorum* is also frequent in the same regions. It can resemble

subsp. *minima* but is easily distinguished by a dark spot in the corolla throat below each lobe, a lack of lanose tomentum and/or cobwebby hairs, and the absence of a distinct basal leaf rosette. It occurs on more fertile soils and in more shaded conditions than does subsp. *minima*.

According to label data, subsp. *minima* occupies gravelly or sandy openings within chaparral, open grasslands, or oak savannah. It frequently occurs among rock outcrops where the topsoil is thin, in dry sandy creekbeds, or in sandy "depressions" within chaparral. It appears to grow in sites that inhibit the competitive growth of associated annual grasses or other weedy taxa; noted associates include several poorly competitive short season annuals including *Minuartia pusilla* and *Pentachaeta exilis*. It has been found from about the latitude of King City in Monterey Co. to the north side of the Cuyama Valley on the boundary of San Luis Obispo and Santa Barbara cos. (Fig. 1). An attempt to locate this taxon in spring 2014 was unsuccessful, likely due to the unusually dry winter of 2013/2014. Some of the listed associates were found in the habitats described, and it may be that subsp. *minima* needs at least a reasonably wet winter to appear in the following spring. Compared to the type specimen, all but a few individuals on the known herbarium sheets are diminutive and suggest that in most years in which it appears at all, the plant may not reach its full vigor and growth potential. Despite the lack of recent collections, subsp. *minima* does not appear to be a particularly rare plant, with the known occurrences spread widely throughout the inner South Coast Ranges (Fig. 1). A note to Alva Day Grant from Clare Hardham, currently in the pocket of *Hardham 5258* (CAS) dated 5-14-60, stated that the plant is "very common-almost as ubiquitous as *Gilia clivorum* … ". In addition to environmental factors that may limit the frequency with which it appears, at least two additional factors contribute to the lack of newer documentation: first, the plants slender stature and sparse foliage make it easily overlooked; and second, its entire known distribution is on private land to which access, since 1960, has become increasingly restricted.

Both subspecies *lanosa* and *minima* occupy the extreme northwestern edge of the *Gilia ochroleuca* complex's distribution. The (probably) outcrossing subsp. *lanosa* is the most narrowly distributed form within the complex, having so far been found only in a remote region of perhaps fifty square miles (Fig. 1). The habitats where it is found are not unlike those of subsp. *exilis* or *bizonata*. Subspecies *lanosa* is an isolated morphological form within *G. ochroleuca*. Its distinguishing features suggest contact and gene flow from other species, particularly those in the *Gilia cana*, *Gilia leptantha*, or *Gilia latiflora* complexes and as such may be a recent result of fluctuating climates in the post-Pleistocene. Its cauline leaves however, suggest an independent derivation of that feature, and subsp. *lanosa* may just as well be a relictual taxon (Lancaster & Kay 2013).

Conversely, the seldom seen subsp. *minima* occupies a wide geographic range, with a north to south distribution of more than 110 miles (Fig. 1). It occupies a low elevation region with an early, short growing season and appears to occupy habitats that are not highly competitive. Its fruits and seeds are on average the smallest and the seeds fewest per locule among the *Gilia ochroleuca* subspecies. To judge from its short-styled, apparently self-fertilizing reproductive system, and adaptation to a short growing season, it may be a recent addition to the increasingly xeric post-Pleistocene conditions of central California.

I offer the following modifications to the dichotomous key by Porter (2012) in The Jepson Manual to account for subspp. *lanosa* and *minima*.

31. Corolla throat yellow or white with five yellow spots at base ..... **Gilia clokeyi, G. opthalmoides**
31. Corolla throat yellow or pale proximally, blue or pale distally.

    32. Corolla 4–7 mm; throat yellow-spotted, </= lobes; calyx lobes short-pointed .... **Gilia clokeyi**
    32. Corolla 7–12 mm; throat yellow >/= lobes; calyx lobes acuminate ..... **Gilia opthalmoides**

33. Stems mostly glabrous below the inflorescence. Without dense ring of short glandular trichomes immed. below the calyx.

34. Basal leaf rachis and divisions narrow, 1 mm or less wide. Basal leaves thinly floccose or +/- glabrous. Lower branches +/- spreading.

35. Corolla 8–14 mm; style > stamens. Calyx glabrous at maturity .....**Gilia ochroleuca** subsp. **bizonata**

35. Corolla 4–6 mm. Style gen. = stamens. Calyx glabrous or cobwebby.

36. Calyx gen. persistently cobwebby, sometimes shedding most of the tomentum in age. Calyx membranes gen. purple or purple-streaked. Stems slender, upright. South Coast Ranges ..... **Gilia ochroleuca** subsp. **minima**

36. Calyx gen. glabrous. Membranes white. Stems slender to stout, spreading or upright. Mojave Desert and margin ..... **Gilia ochroleuca** subsp. **ochroleuca**

34. Basal leaf rachis and divisions broader, 2–4 mm wide. Basal leaves generally densely cobwebby tomentose. Plant low, stems spreading ..... **Gilia ochroleuca** subsp. **vivida**

33. Stems densely to partially floccose below the first inflorescence branches. A +/- dense ring of short-stalked glands freq. present on pedicels immediately below the calyx.

37. Plant scapose, simple or branched weakly above the base, strictly upright. Basal leaves 1–2 pinnate with 2–3 mm wide divisions and rachis. Stems densely lanate, (less by late maturity); terminal lobe of cauline lf. elongated, lanate, lanceolate-linear, with 1–2 pairs of short deltate to lanceolate divisions near base, in length 1–3 times the rachis width ..... **Gilia ochroleuca** subsp. **lanosa**

37. Plant gen. with multiple branches from the base, the lower spreading. Basal leaves 0–2 pinnate with narrow, 1 mm wide divisions and rachis, or leaves simple. Stems cobwebby in the lowermost parts, the lower and middle cauline leaves thinly lanate or glabrous terminal lobe similar to the laterals, with 2–3 pairs of elongate linear divisions, their length 3–10 times the rachis width ..... **Gilia ochroleuca** subsp. **exilis**

ACKNOWLEDGEMENTS

Much appreciation to the curators and staffs at RSA-POM, CAS-DS, DAV, SBBG and UC for loans of specimens. The US Dept. of the Interior generously provided multi-year collecting permits for the San Rafael Wilderness and the US Forest Service provided similar permissions for the author to collect on the lands under their jurisdiction. Many thanks to Matthew Beyers for field assistance in the San Rafael Wilderness and Robert M. Rhode for editorial consultation. Thank you to Riad Balbaaki and Scott Kinnee of the CDFA Plant Pest Diagnostics Laboratory for their expert help with the type photographs and SEM micrographs. Special thank-you to Debra Trock of the California Academy of Sciences for work space and the photograph of the type of *Gilia pedunculata* var. *minima*. Last, but not least, to editor Guy Nesom for his critical reading and stimulating discussion of the issues of taxonomic rank in relation to evolutionary status in this and other plant groups. These discussions markedly improved this report.

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